

# KIMMERIDGIAN METRIORHYNCHID CROCODILES FROM ENGLAND

by DANIEL R. GRANGE *and* MICHAEL J. BENTON

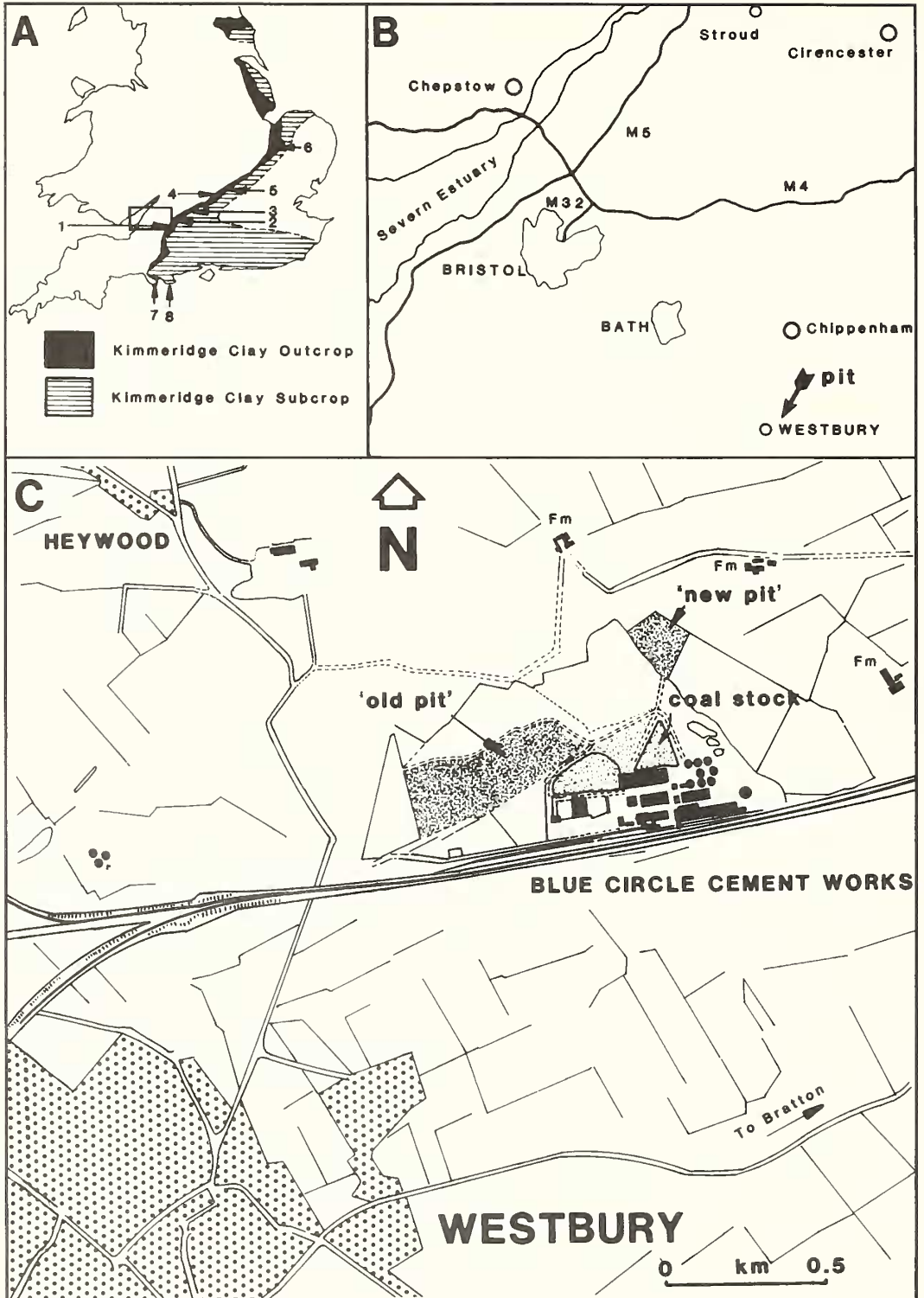
**ABSTRACT.** Remains of metriorhynchid crocodylians are rare in the British Kimmeridgian. A new partial metriorhynchid skull, recently discovered at Westbury, Wiltshire is provisionally assigned to *Metriorhynchus superciliosus*, a common narrow-skulled species previously described from the Oxford Clay (Callovian) sequences of Peterborough. It is covered with encrustations on both dorsal and ventral surfaces, indicating a long period of exposure on the sea floor, in relatively oxic conditions, before burial. There is evidence for both predator damage and a phase of post-depositional deformation.

METRIORHYNCHID crocodylians are known from the Middle Jurassic (Bathonian) to the Lower Cretaceous (Hauterivian) of England, France, Germany and Switzerland (Steel 1973; Benton 1993). Primitive metriorhynchids include *Pelagosaurus* from England and France (Buffetaut 1980). The Bathonian record is *Teleidosaurus* from France (Benton 1993). Large quantities of metriorhynchid material were recovered from the lower Oxford Clay (Callovian) brick pit exposures of the Peterborough district, eastern England (Andrews 1913; Leeds 1956; Martill 1986). Callovian metriorhynchids are also abundant in northern France, Germany and South America (Steel 1973; de Gasparini and Diaz 1977). Material from these discoveries have been ascribed to 20 or more 'species' of *Metriorhynchus*. Oxfordian metriorhynchids are rare, with a record from France (Martill 1991). Kimmeridgian forms, including *Metriorhynchus* and *Dakosaurus*, have been reported from England and France (Benton 1993; Benton and Spencer 1995). Portlandian metriorhynchids include *Dakosaurus* and *Geosaurus* from Germany, and Lower Cretaceous (Neocomian) specimens are known from France, northern Germany and Italy (Steel 1973).

Metriorhynchids are distinguished from other Mesozoic crocodylians by their aquatic adaptations. They were the only archosaurs that became specially adapted to a marine habitat (Neill 1971). They possess reduced, web-like, fore- and hind-limb extremities, a streamlined skull and a laterally compressed tail that enabled efficient long-range swimming (Martill *et al.* 1994).

The Kimmeridge Clay of England crops out in a long narrow strip running from Dorset in the south-west to Yorkshire in the north-east (Text-fig. 1A), with fossil reptiles reported from more than 60 localities (Benton and Spencer 1995). The commonest discoveries include ichthyosaurs, such as *Grendelius*, *Macropterygius*, *Nannopterygius* and *Ophthalmosaurus*, and plesiosaurs, such as *Colymbosaurus*, *Kimmerosaurus* and *Pliosaurus* (Brown 1981; Taylor and Cruickshank 1993). Rare discoveries include turtles (*Pelobatochelys*), pterosaurs (*Geruaodactylus*), dinosaurs ('*Megalosaurus*'), and crocodylians (*Metriorhynchus*). The purpose of the present paper is to describe a new metriorhynchid skull from the Kimmeridgian of Wiltshire, and to review other English Kimmeridgian metriorhynchid specimens. The new specimen is provisionally assigned to *Metriorhynchus superciliosus* (de Blainville, 1853) pending a revision of metriorhynchid taxonomy being undertaken by the senior author.

Repository abbreviations used: BMNH, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD; BRSMG, Bristol City Museum and Art Gallery, Queens Road, Bristol, BS8 1RL; CAMSM, Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ; OUM, Oxford University Museum, Parks Road, Oxford, OX1 3PW.



## DESCRIPTION OF THE WESTBURY SKULL

*Locality and stratigraphy*

The *Metriorhynchus* skull from Westbury, Wiltshire (BRSMG Ce17365) was discovered on 30th December 1991, by Mr S. Carpenter in the 'old quarry' at the Blue Circle Industries plc Westbury Works, Wiltshire (NGR ST 8817 5267) (Text-fig. 1B-C). It lay *in situ* 1 m below the *Crussoliceras* limestone marker (*Aulacostephanus eudoxus* Zone (E6), Lower Kimmeridge Clay, of Birkelund *et al.* 1983) (Text-fig. 2).

The skull lay upside-down on a bedding plane surface, with the damaged posterior portions exposed in the section of the pit face. The remains had to be excavated rapidly, owing to the risk of further disturbance. The skull was contained in a large block of clay, which fragmented into three smaller pieces when an attempt was made to lift it. These pieces, and isolated bone fragments in the area, were collected (S. Carpenter, pers. comm. 1994).

*Preparation and conservation*

The blocks containing the *Metriorhynchus* skull were kept damp during transport to the conservation laboratory at Bristol City Museum and Art Gallery. The conservator was able to remove excess clay using a palette knife and scalpel. Distilled water and a brush were used to wash away the remaining dirt from the bone surfaces. Following this initial separation work, the skull elements were consolidated and reconstructed. A solution of Paraloid B72 dissolved in acetone was used for both surface consolidation (10 per cent Paraloid B72 in acetone) and as an adhesive (60 per cent Paraloid B72 in acetone) (D. B. Hill, pers. comm. 1994).

*General description*

The skull is fragmented, especially in the medial areas of the rostrum (Text-figs 3-5). There are numerous fractures over the surface of the skull some of which obscure surface features such as sutures. Several portions of the skull are missing, either as a result of erosion processes after the animal had died or by their being smashed at the site of discovery by quarry machinery and subsequently lost. Such missing areas include the nasal margins and portions of the snout. The majority of the braincase seems to have been lost prior to burial, as no attachment surfaces are present. The mandible is also missing. The skull is dorsoventrally flattened, and there has also been lateral compression.

The general skull shape is typical of the Metriorhynchidae (Andrews 1913); elongate, with large temporal fenestrae, a well-developed nasal area, and little lateral expansion of the premaxillae. The major dorsal openings are nowhere fully delimited. The form of the heart-shaped narial aperture, although incomplete, can be discerned from the median posterior and anterior processes and lateral margin of the left premaxilla. Both orbital openings are defined anteriorly by the prefrontals and medially by the frontal, but the lateral boundaries are missing. The posterior margin of the right orbit borders the postfrontal bar, but this is absent on the left.

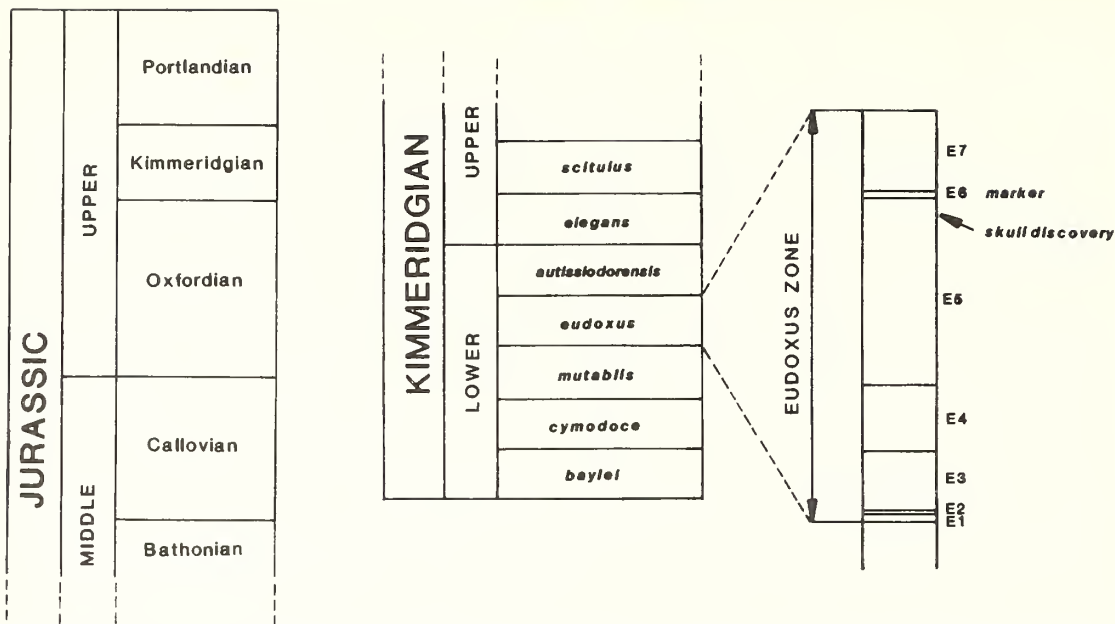
The temporal fenestrae are unusually large, far larger than those of Callovian metriorhynchids (Andrews 1913) and of the Kimmeridgian skull from Oxfordshire (OUM J.29823; Pl. 1). The right-hand fenestra is more defined than the left, as the postfrontal is complete on that side. Medially the fenestrae are bounded by the narrow frontal/parietal crest, but the posterolateral extensions of the parietal are missing.

*Dermal elements of the skull roof*

*Premaxilla.* The premaxilla on the left side is preserved, except at its anteroventral extremity where breakage has occurred. The right-hand element is largely absent (Text-figs 3-4). The border of the narial opening on the left-hand side is a shelf-like projection, which thickens anteriorly from a thin posterior concave embayment.

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TEXT-FIG. 1. Kimmeridge Clay metriorhynchid crocodylian sites in England. A, map showing the Kimmeridge Clay outcrop and subcrop, with main metriorhynchid localities indicated. Numerical key: 1, Westbury (Wiltshire); 2, Devizes (Wiltshire); 3, Swindon (Wiltshire); 4, Wootton-Bassett (Wiltshire); 5, Shotover Hill, Heddington, Garsington (Oxfordshire); 6, Ely (Cambridgeshire); 7, Weymouth (Dorset); 8, Kimmeridge Bay (Dorset). B-C, maps showing the location of Blue Circle Industries plc, Westbury Works.



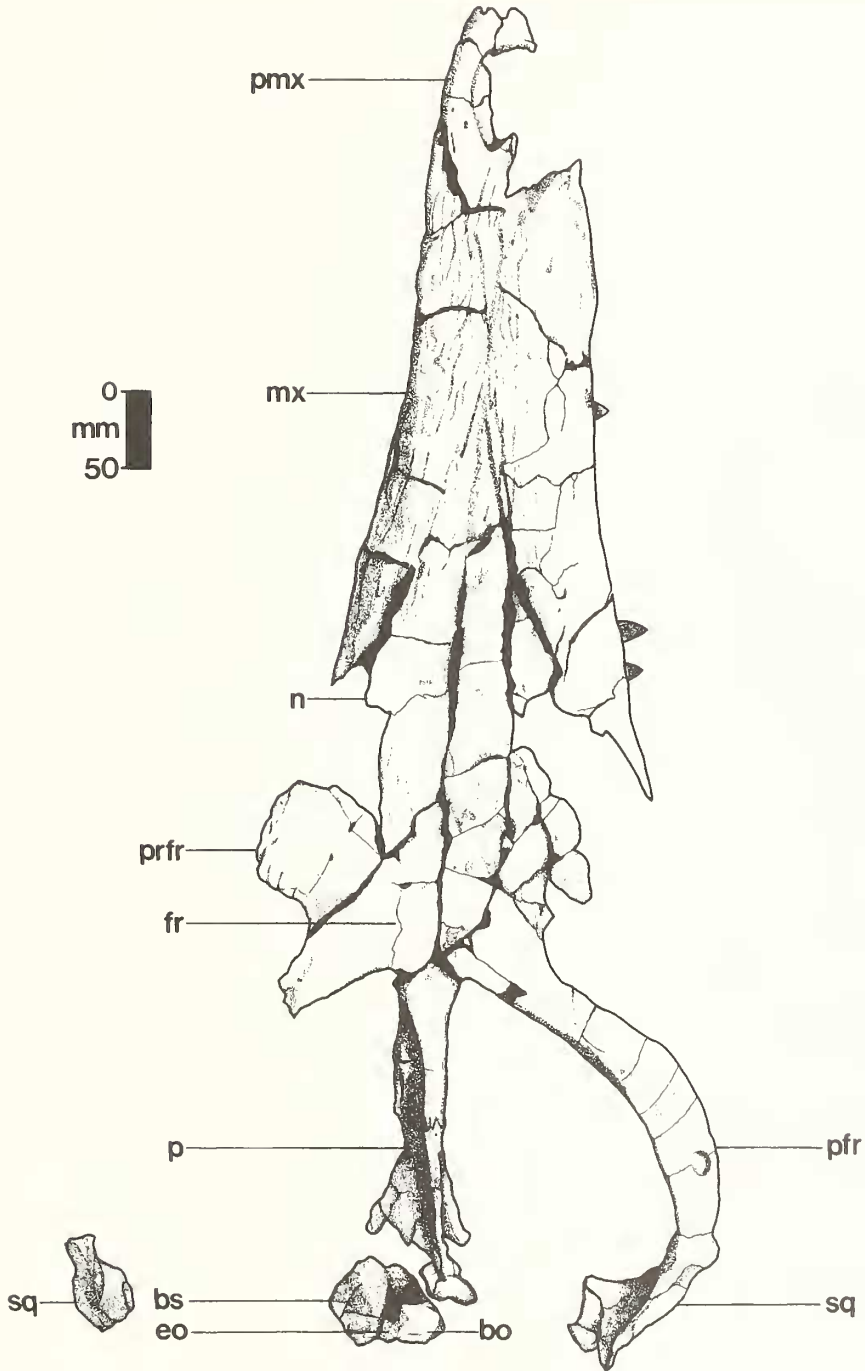
TEXT-FIG. 2. Biostratigraphical divisions of the Kimmeridgian and portion of the section at Westbury pit, showing the horizon of the metriorhynchid skull. Based on Birkelund *et al.* (1983) and Hallam (1992).

The anterior edge curves inwards to form the anterior margin of the narial opening. On the left side, the suture between premaxilla and maxilla is deep and ornate, and runs obliquely to join the deep furrow of the midline suture. The line of this suture on the right-hand side is barely discernible, and it appears to represent a line of weakness along which the skull has broken. The thick lateral surface of the left premaxilla is well preserved, and shows microfracturing and pitting, especially on the dorsal surface of the bone, but this diminishes laterally and posteriorly. The pits range from 0.5–5 mm in length, with a modal value of 1 mm. Most of the pits are ovate, the remainder subcircular. A preferred orientation is apparent, with the long axes trending approximately parallel to the midline of the skull.

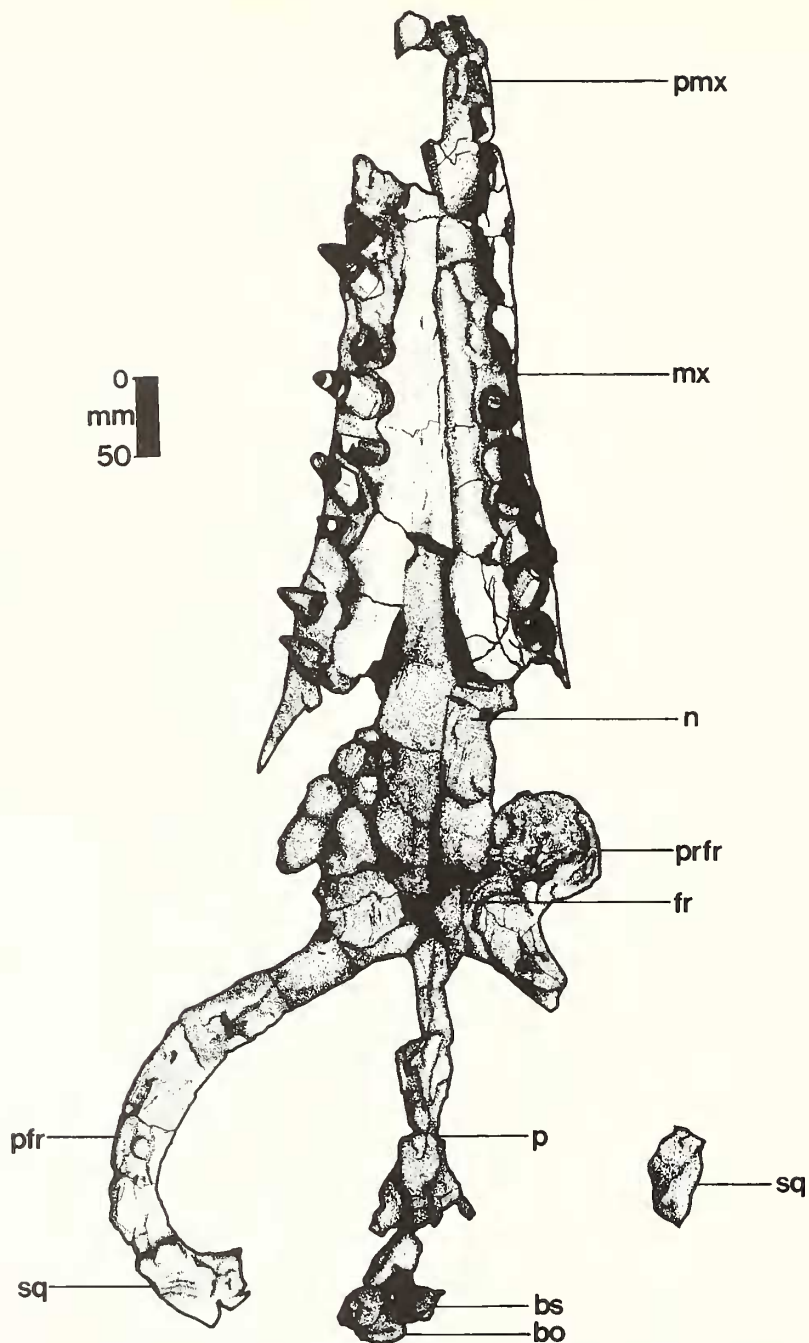
*Maxillae.* Both left and right maxillae are present. Most of the left maxilla is complete, except for the posterior margin, where weathering has occurred along the suture line with the nasal. This is also the case with the right-hand side. The suture between the maxilla and nasal is smooth, and is marked by a deep groove which joins the medial suture in a sharp 'V'-shaped wedge (Text-figs 5A, 6A). Posteriorly, on either side, the suture is obscured because of breakage, and in these areas the contact with the frontal is absent. Both maxillae have been distorted. The lateral region of the right maxilla has been flattened dorsoventrally with respect to the left maxilla. The latter is thickened and overturned, verging towards the left side. In the area of convergence between the maxillae there has also been thickening on the right side, adjacent to the line of the midline suture. Both maxillae, and both nasals, have rolled inwards towards the midline, when seen in dorsal view (Text-fig. 6A), forming two convex surfaces which bound a 'V'-shaped depression, on what should really be a simple convex dorsal snout surface.

The maxillae show a great concentration of surface markings (Text-fig. 6A), a feature noted also in the Callovian specimens described by Mateer (1974). Grooves deviate from the midline suture on both sides and run obliquely, following the line of the maxilla/nasal suture. They are more pronounced on the left maxilla, but fade approximately half-way along the maxilla/nasal suture on either side. The grooves are discontinuous, ranging from 9–47 mm in length (modal value *c.* 25 mm), and less than 3 mm in width. Surface furrows are seen also at the anterior end of the left maxilla, running back from the premaxilla, but these are less clear on the right-hand side. Pitting on the right maxilla is more pronounced than on the left. On the latter, the pits are shallow and tend to merge with grooves, making distinction between the two extremely difficult. Anteriorly,



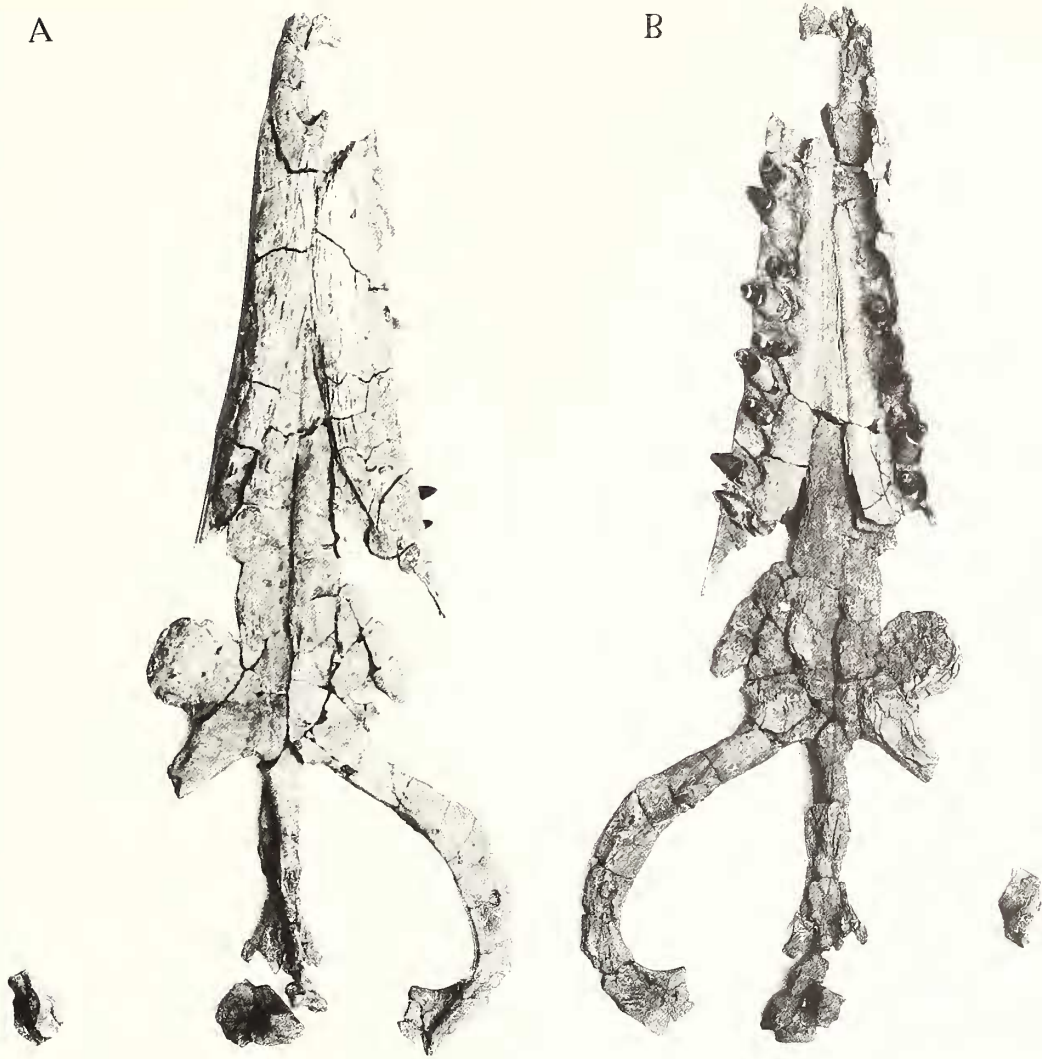


TEXT-FIG. 3. *Metriorhynchus superciliosus* de Blainville, 1853; skull (BRSMG Ce17365); dorsal view. Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; fr, frontal; mx, maxilla; n, nasal; p, parietal; pfr, postfrontal; pmx, premaxilla; prfr, prefrontal; sq, squamosal.



TEXT-FIG. 4. *Metriorhynchus superciliosus* de Blainville, 1853; skull (BRSMG Ce17365); ventral view. Abbreviations as in Text-figure 3.

the pits in the medial area have their long axes aligned parallel to the midline suture, and these diverge posteriorly, following the orientation of the maxilla/nasal suture. Pits near the lateral margin of the right maxilla are large and ovate, with long axes reaching 10 mm, and they become almost furrow-like posteriorly.



TEXT-FIG. 5. *Metriorhynchus superciliosus* de Blainville, 1853; skull (BRSMG Ce17365). A, dorsal view; B, ventral view;  $\times 0.16$ .

The ventral surfaces of the maxillae are characterized by fine, longitudinal ridges trending parallel to a marked medial suture (Text-fig. 6B). Either side of the suture, convex surfaces are present adjacent to the dentition. Randomly distributed minute pitting is present on both sides, but fades adjacent to the teeth.

*Nasals.* Both nasals are present, but the posterolateral regions are missing. The suture between the nasal and the pre-frontal differs on the two sides on the right side, it is relatively straight to the contact between nasal and frontal, since the prefrontal has been compressed laterally, but on the left the suture would have been curved. The nasal/frontal suture is highly ornate and incised in front, and it curves back laterally towards the prefrontal. It is best preserved on the right-hand side. The nasal surfaces are relatively smooth, with occasional pitting anteriorly.



TEXT-FIG. 6. *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, maxillary/nasal surface (note suturing and sculpturing). B, dentition. Scale bar represents 50 mm.

*Prefrontals.* Both prefrontals are present, but the anterior, lateral, and posterior margins are missing. The prefrontals form thick anterior borders to the orbits, a feature typical of the metriorhynchids (Mateer 1974). These elements show further evidence of the horizontal deformation event which affected the maxillae and nasals. The right prefrontal is narrow and elongate as a result of compression, whereas the left prefrontal is sub-circular. The left prefrontal is laterally thickened and convex, indicating that it has been compressed to a certain degree. The surfaces are pitted.

*Frontal.* The frontal is complete, but highly fragmented, especially to the right of the midline suture. The frontal/prefrontal suture, seen only on the right-hand side, is ornate on a fine scale, but retains an approximate straight line. The frontal crest rises slightly to meet the parietal ridge in a highly ornate and incised suture, which is complex, but not fused (Text-fig. 3). This suture may be traced laterally down the right-hand side of the ridge flank, where it ends abruptly at a break in the bone on the inner margin of the temporal



fenestra. It is not so extensive on the left-hand side. The smooth frontal surface is interrupted by occasional pitting and fracturing. Fine striations radiate outwards from the midline towards the lateral margins.

*Parietal.* The parietal is broad anteriorly, and narrows posteriorly into a sharp ridge. The frontal/parietal suture is preserved on the ventral surface, but is weathered anteriorly and posteriorly. Fine longitudinal furrows and ridges extend both anteriorly and posteriorly from the suture, but eventually fade. The lateral compression of the skull has twisted the frontal/parietal crest towards the left in the medial and posterior region. The top of the crest is overturned towards the right, overhanging the temporal fenestra, and forming a broad concave left edge on the flank of the crest. Surface features are inconspicuous.

*Postfrontal bar.* The postfrontal bar is present only on the right-hand side (Text-figs 3–4). It is sutured with the frontal anteriorly, and with the squamosal posteriorly. The squamosal suture is ornate and deeply incised, but weathered. The postfrontal broadens along its outer curved edge and narrows towards the posterior suture. It is devoid of surface markings. Approximately half-way along the postfrontal, a large (16 mm) oval pit is present (Text-fig. 7A). Ventrally, the postfrontal surface is weathered in certain areas. The suture with the frontal can be seen anteriorly, although the preservation is poor, and the suture with the squamosal is difficult to follow.

*Squamosal.* The squamosal is incomplete on the right-hand side, and only a small piece exists on the left, which is weathered on its lateral edge. A sharp ridge runs down on the medial surface of the right squamosal, from the suture with the postfrontal to the end of the bone, showing the same sense of distortion as described for the parietal ridge. The squamosal surfaces on either side of the ridge are occasionally pitted and slope gently away towards the inner margin, and abruptly on the outer margin.

#### *Dermal bones of the palate*

All traces of the posterior palate elements are missing, as is the palatal portion of the premaxillae. The secondary palate formed by the junction of the maxillae in the midline is, however, nearly complete (Text-fig. 6B), and shows a long, straight, midline suture. As in other metriorhynchids, the posterior portion of the secondary palate was presumably formed by the palatines (Andrews 1913), which met in the midline behind the maxillae. The vomers were reduced and close to the midline above the secondary palate. There is no trace of these elements, nor of the pterygoids.

#### *Endocranium*

The basioccipital is the most prominent element of the braincase (Text-figs 3–4), showing the characteristic central depression and ventrally necked process. Below, the arched median eustachian opening is present, which defines laterally the innermost abraded margin of the exoccipital. Dorsally, the supraoccipital and parietal contacts are absent. The quadrate and epipterygoid are not preserved.

Anteriorly, the basisphenoid is only partly complete and is badly abraded, with the exception of a small section on either side of the midline. The bone is displaced to the left of the basioccipital, a further result of the compressional event that affected the skull.

#### *Dentition*

The dentition on both sides of the maxillae is robust (Text-fig. 6B). Nine teeth are present on the right maxillary margin, of which seven are complete. Two teeth in the process of eruption can be seen towards the rear of the tooth row as a result of breakage of the bone. Four teeth are present on the left maxillary margin, of which only one is complete. Four alveoli are preserved, with intervening convex ridges, and one bearing the remains of a tooth. The premaxillary margin has the remains of a tooth lying on its side over a depression, which possibly represented its socket.

The maxillary teeth conform to the typical metriorhynchid shape (Massare 1987), having laterally compressed pointed crowns, defined anteriorly and posteriorly by prominent carinae. The enamel displays fine longitudinal ridges that become coarser away from the smooth apex, until they end abruptly at the gum tissue boundary. The cross section of the teeth varies with size: large teeth are sub-circular, whereas smaller teeth are more ovate and laterally compressed.

Although only one wear facet is present, which probably resulted from abrasion on an opposing tooth, the apices of the teeth are highly polished, possibly indicating abrasion from hard prey (Massare 1987).

### *Nerve and vessel openings and other surface features*

Many elements of the skull show openings, which have been described. They may be interpreted by reference to presumably homologous nerve and vessel positions in the skulls of modern reptiles, such as crocodylians (Iordansky 1973) and *Sphenodon punctatus* (O'Donoghue 1920).

The conspicuous foramina along the lateral margins of the maxillae are positioned adjacent to each tooth (or tooth socket) on both sides of the snout. These may be openings for accessory nerves to teeth and gum tissues from the *Ramus maxillaris* extension of the trigeminal nerve system. The *R. maxillaris* runs from the braincase laterally to musculature in the temporal fossae (*M. pseudotemporalis*) and dorsally to pterygoid musculature (*M. pterygoideus anterior*), and then into the upper jaw region (Romer 1956; Schumacher 1973).

The foramina on the premaxillary surfaces are likely to have accommodated the superior and inferior *Arteria nasalis*, the terminal branches of which supply the nasal tissues (O'Donoghue 1920). The *A. nasalis* is an anterior extension of the *A. orbitalis superior*, which accompanies the *R. ophthalmicus* trigeminal nerve branch, from the main *A. stapediales*. The *A. orbitalis superior*, and associated rami supplying orbital muscles (Romer 1956), may have caused the pitting on the pre-frontal surfaces which overhang the orbits and the minor pitting on the anterior and posterior areas of the nasal. However, the frontal pitting is more probably attributable to the *A. frontalis*, running upwards from the posterior region of the orbit to supply superficial tissues (O'Donoghue 1920).

Observations on modern adult crocodylians (Iordansky 1973) reveal a network of irregular ridges on the dorsal surfaces of the dermal skull elements, creating a 'sculpturing effect', caused by osteodermal accretion. This is possibly the reason for the linear sculpturing present along the length of the premaxilla and maxillae, where presumably there was little demarcation between the integument and skull surface (Steel 1989). Langston (1973) noted, however, that fossil taxa exhibiting the greatest degree of aquatic adaptation possess the least osteodermal accretion.

The large ovate cavity situated on the postfrontal bar (Text-fig. 7A) is problematical. It is almost certainly not a vessel opening, and may represent predator damage, inflicted before or after death. Predatory marks with a similar appearance, are present in Kimmeridgian marine reptile specimens from Kimmeridge Bay, Dorset (S. Etches Collection, pers. obs. DRG).

## OTHER ENGLISH KIMMERIDGIAN MARINE CROCODYLES

### *The Oxford skull*

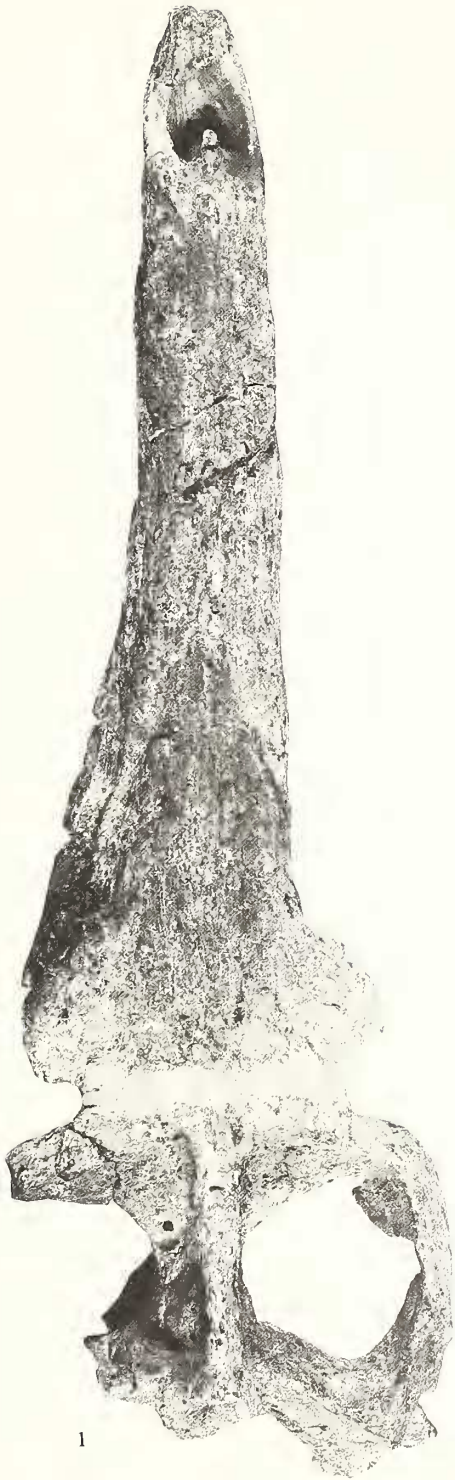
A partial skull and incomplete lower jaw from the Kimmeridge Clay pits of Shotover Hill, Oxfordshire (OUM J.29823) was mentioned by Owen (1884) and was made the type of *Steneosaurus palpebrosus* by Phillips (1871). It was re-identified as a metriorhynchid by Woodward (1885).

The temporal openings (Pl. 1) are small and circular, and are bordered anteriorly and laterally by wide, embayed shelves. The maxillary region shows distortion in a dorso-ventral plane. Suturing on the dorsal surface is marked in certain areas. A midline suture is apparent on the skull table and maxillary surfaces; it terminates in the medial portion of the frontal, but continues anteriorly across the nasal area, and along the majority of the anterior portion of the maxilla, but does not reach the posterior border of the premaxilla. A deeply incised groove defines an elevated and wide skull table, with a reduced nasal area. The unusually small nasal is approximately 100 mm in length, and is separated from the frontal by a sinuous suture, which transects the major division between the frontal and maxillae. The prefrontals are characteristically robust, and laterally, the lachrymals, and their corresponding foramen, are preserved. Other elements, such as the prefrontals and premaxillae, are bordered by faint sutures that are only apparent upon close inspection. The parietal crest is narrow and high. Dorsal surfaces have an unusual, roughened texture, which commonly obscures the suturing and sculpturing. There are no visible macro-epibionts.

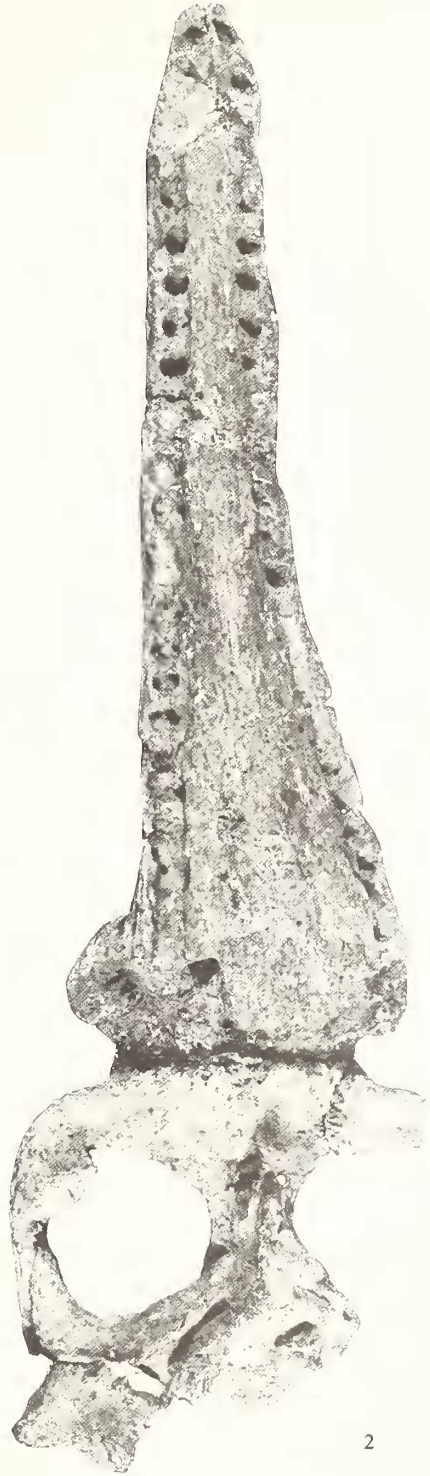
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### EXPLANATION OF PLATE I

Figs 1–2. *Metriorhynchus palpebrosus* Woodward, 1885; OUM J.29823, Kimmeridge Clay, Shotover Hill, Oxfordshire. 1, dorsal view; 2, ventral view;  $\times 0.4$ .

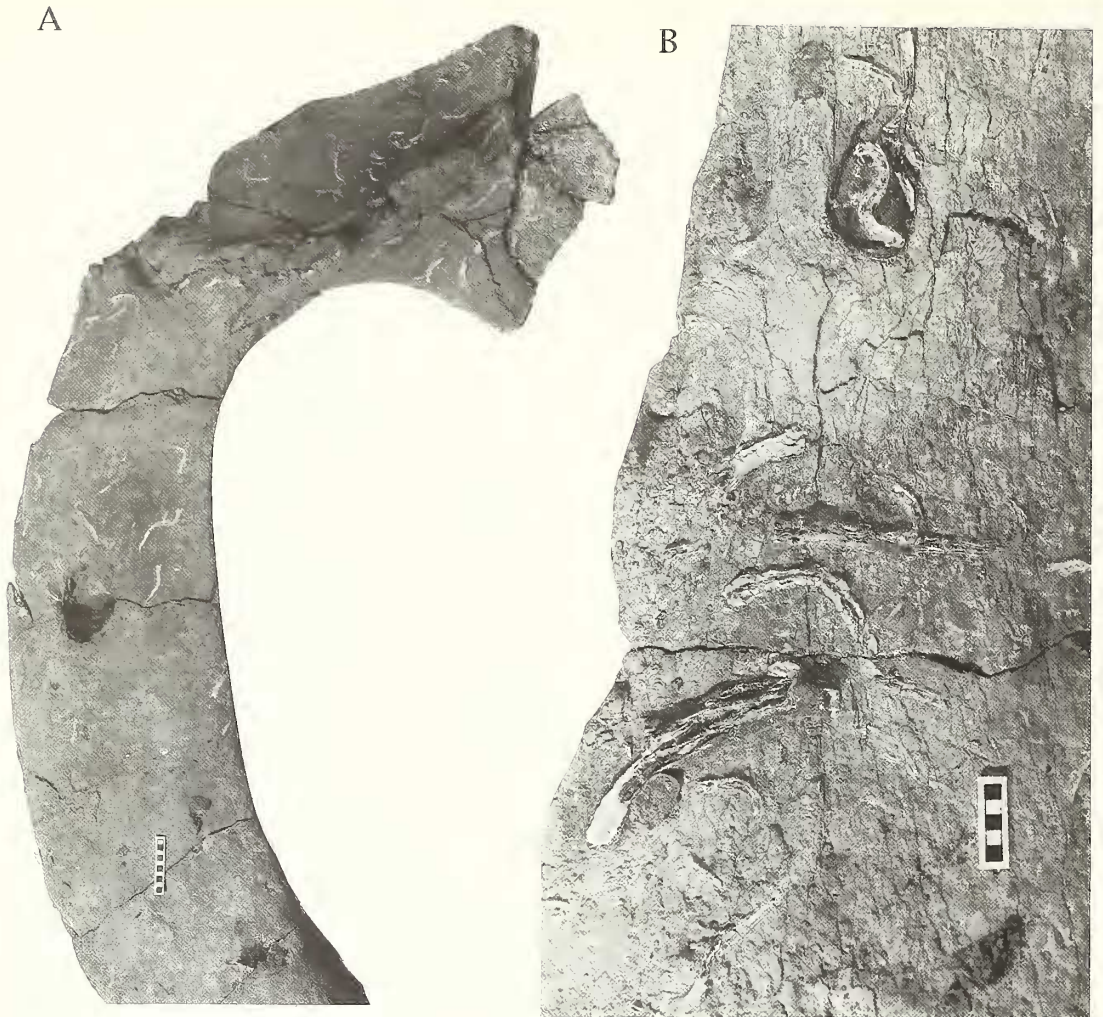


1



2





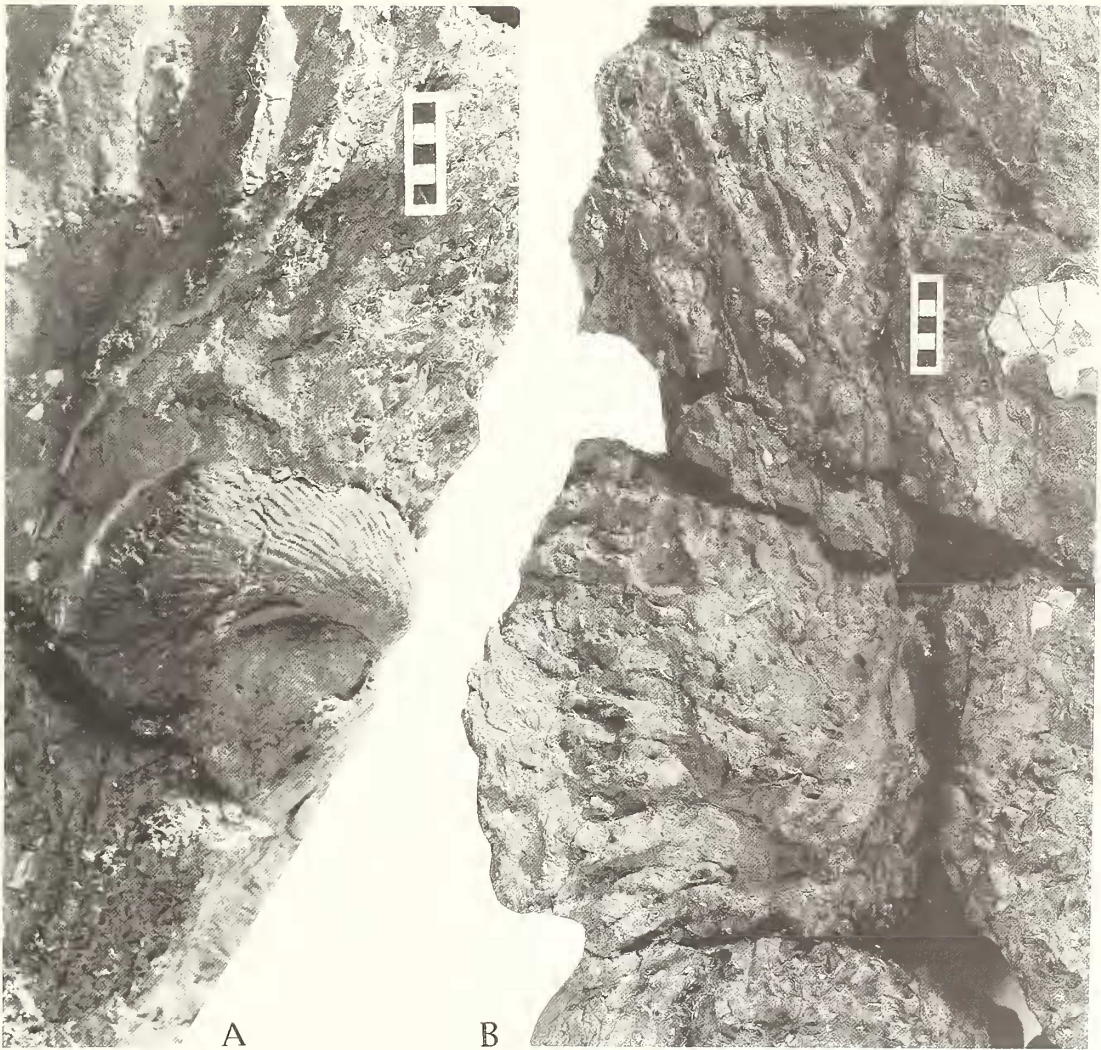
TEXT-FIG. 7. *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, predator damage on right-hand postfrontal; scale bar represents 10 mm. B, medial portion of left-hand nasal (note oyster and serpulid encrustations); scale bar represents 5 mm.

On the ventral surface of the skull (Pl. 1, fig. 2), there are 23 alveoli on the right margin, and 25 on the left. No teeth are preserved. Although the posterior margin of the palate is weathered, two internal narial openings are well defined. The inner face of the jugal is partially preserved on the right-hand side, represented by an inwardly directed process attached to the ventral surface of the postfrontal. The pterygoid and parasphenoid are missing, but posteriorly the occipital area is preserved. On the right posterior margin of the skull, the mandibular condylar surface of the quadrate is present, and the contact with the squamosal is seen. The equivalent elements on the left-hand side are missing.

#### *The Dorset skull*

A lower jaw and various skeletal fragments from the Lower Kimmeridge Clay of Kimmeridge Bay, Dorset (BMNH 40103) were described and identified as *Dakosaurus maximus* (Hulke 1869). This material was





TEXT-FIG. 8. *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, *Nanogyra?* sp., encrustation on ventral surface of right-hand postfrontal; scale bar represents 5 mm. B, *Stomatopora?* sp., encrustation on ventral surface of left-hand prefrontal; scale bar represents 5 mm.

subsequently re-identified as *Steneosaurus manseli*, following the recognition of a partial skull of the same individual at this locality (Hulke 1870). Owen (1884) referred this species to the new genus *Plesiosuchus*, but Woodward (1885) retained it in *Dakosaurus*, a metriorhynchid genus. Hulke (1870) assigned the material to *Steneosaurus* because of its apparent similarity to the Oxford skull, before the reidentification of the latter by Woodward (1885). Fraas (1902) further described the skull form of *D. manseli* from a specimen from this locality.

Lydekker (1889, 1890) noted teeth and scutes of *Metriorhynchus* from Smallmouth Sands, Weymouth. However, it is well known that metriorhynchids lacked dermal armour (Andrews 1913), and therefore this identification is erroneous. Other possible metriorhynchid material from the Kimmeridgian of the Dorset coast has been reported. Delair (1958) refers to 'teeth and some vertebral centra of several individuals from the Kimmeridgian of Weymouth' (BMNH 43032, 44179, 46805a, b, c, 49511). Isolated metriorhynchid limb, skull

and vertebral column elements have been identified from Swindon, Devizes and Wootton-Bassett (Wiltshire), Ely (Cambridgeshire) and Shotover Hill, Headington and Garsington (Oxfordshire) (Text-fig. 1A) (OUM J.12367, J.12373, J.55470–J.55479; BMNH 24803, 24805, 31920, 46492; CAMSM J.67879–J.67899). These fragments are generically indeterminate (pers. obs., DRG), because they are unsuitable for identification purposes. It is quite possible that misidentification by previous workers has occurred.

Taylor and Benton (1986) noted two disarticulated crocodylian finds from the Upper Kimmeridge Clay of Egmont Bight on the Dorset coast, one of which at least (R. A. Langham Collection) is a metriorhynchid (see also Benton and Spencer 1995).

### *The Ely skull*

A partial skull (CAMSM J.29419) from the Kimmeridge Clay of Ely, Cambridgeshire, was identified as *Dakosaurus lissocephalus* by Seeley (1869). Indeterminate material, including skull bones, jaw fragments, vertebrae, ribs, pectoral and pelvic girdle elements and limb bones, is possibly associated with the skull (Seeley 1869) (CAMSM J.29383–J.29418; J.29420–J.29446). The species *Metriorhynchus hastifer* Eudes-Deslongchamps, 1868, was identified by Watson (1911) on the basis of the anterior end of a snout.

## TAPHONOMY OF THE WESTBURY SKULL

The Westbury skull is encrusted to varying degrees with diverse macro- and micro-epibionts. During pre-burial, and possibly after sediment covering, the skull surfaces provided a site for scavenging epibiont communities. Micro-epibionts are the most abundant encrusters on both dorsal and ventral surfaces, and in the surrounding sediments (Birkelund *et al.* 1983). There is evidence for surface scavenging in all epibionts, and scavenging between communities is also evident in certain areas.

*Macro-epibionts.* Serpulid polychaetes are present on the dorsal surfaces of all skull elements (Text-fig. 7B), particularly in the maxillary and nasal region, but they are rarer on the ventral face of the skull. Serpulids also encrust the argillaceous matrix within bone cavities where breakage had occurred, thus providing evidence of skull fragmentation before burial. They are preserved as white calcareous tubes exhibiting various degrees of curvature.

Both partial and complete 'oyster' shells (*Nanogyra?* sp.) are present on both dorsal and ventral surfaces (Text-fig. 8A), but mostly on the former. The majority are small, with shells no wider than 10 mm, and virtually all are disarticulated. They often have a close spatial association with the serpulid polychaetes. Many of the shells are abraded and it is often difficult to identify surface features such as growth lines. Shells in the vicinity of the midline suture have been overturned on to their edges as a result of the lateral distortion.

A large bryozoan colony (*Stomatopora?* sp.) encrusts the ventral surfaces of the postfrontal, prefrontals (Text-fig. 8B) and nasal. Most of the colony is abraded, but zooecial apertures are still well defined in certain areas.

*Micro-epibionts.* Cytheracean ostracods (order Podocopida) occur commonly in small clusters, and on the dorsal surfaces are often found in close association with oyster shells and serpulid polychaetes. The ovate dorsal convex margins are preserved, being highly impregnated with pore canals and creating a strong framework structure. The lateral selvage and dorsal hinge line can be seen where weathering of the carapace has not occurred, and the posterodorsal caudal process is also visible in certain instances. Inner surfaces of the valve are also discernible in certain examples, where a median sulcus and hinge line are preserved.

Rotaliine foraminifera are extremely abundant on the ventral surface of the maxillae and nasals, often occurring in clusters. Preservation varies considerably, from abraded and often indistinct tests, to an extremely well defined condition. In most cases, the planispiral perforated test form, with its prominent proloculus, is evident. A nodosariacean foraminiferan (*Lenticulina?* sp.) is the most



abundant rotaliine on the skull surfaces. It possesses an involute planispiral form with lenticular growth, and the test surface is finely perforate with a reticulate sculpture. A lateral keel is also visible.

Textulariine foraminifera are also present. However, these are uncommon compared with the Rotaliina. They are multilocular, and therefore belong to the superfamily Lituolacea. The best preserved specimen (*Trochammina?* sp.) has globular ovate chambers, a deep umbilical region and shows trochospiral growth.

*Interactions between epibionts.* Evidence of fouling is apparent where serpulid polychaete tubes and 'oyster' shells have encrusted upon each other. Reciprocal overgrowth (Taylor 1990) is present where an 'oyster' shell clearly overlaps a serpulid polychaete tube in one area, but has one of its edges overlapped by the same polychaete tube in a different area. These two epibionts are also seen to have marginal contacts, where no overgrowth is observed at all (Text-fig. 7B). Ostracods, often in small clusters, foul the serpulid polychaete tubes, and are also found in close proximity to 'oyster' shells.

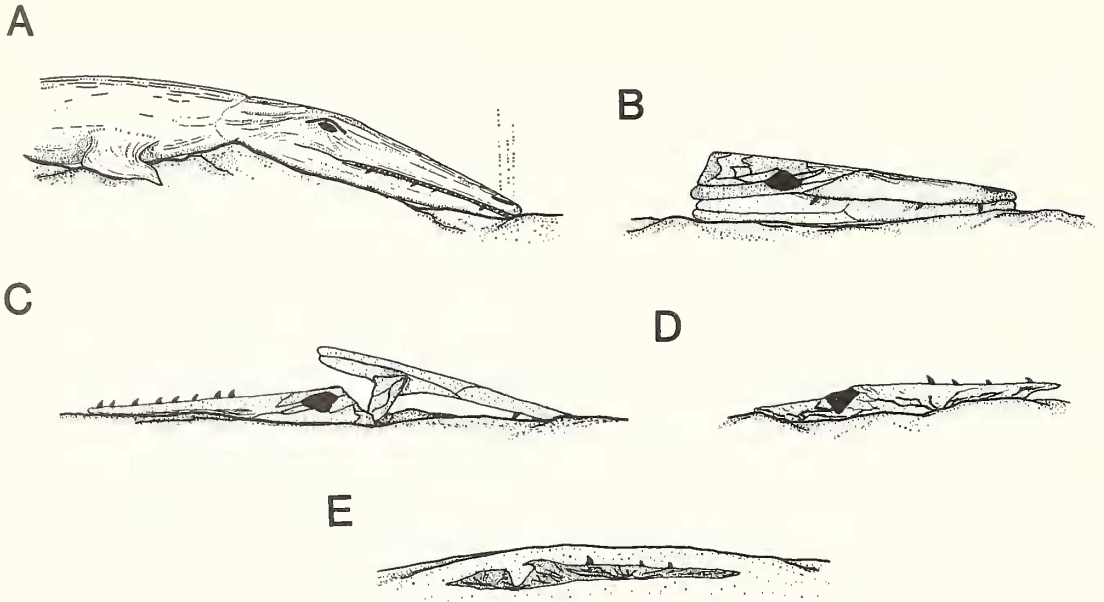
The close spatial relationship between these epibionts indicates competition for space on the skull substrate. Concentrated encrusted areas are situated on the lateral margins of the maxillae, the anterior regions of the nasal, and the left prefrontal. This clustering was possibly caused by local environmental forcing, associated with small-scale storm events (Wignall 1989) in the vicinity of the skull. The organisms were periodically driven on to relatively stable areas devoid of muddy sediment. Ostracods thrive in such environments (Brasier 1980), and this is substantiated by their numbers on both dorsal and ventral surfaces of the skull. The close association of ostracods with other epibionts suggests that they possessed a filter-feeding habit.

The above relationships suggest that there was no community hierarchy on dorsal or ventral substrates during colonization. Even if there was more substantial evidence of hierarchical encrustation, this would only present a snap-shot of a long-term colonization history, the outcome of which would be uncertain, because of complications such as rank reversals and colony recovery after overgrowth, as recorded in modern environments (Buss 1986).

*Taphonomic history.* After initial settling of the carcass (Text-fig. 9A), disarticulation of the skull probably occurred while the body floated, buoyed up by gases generated by degradation of supporting tissues (Schäfer 1972). However, the extent to which this can occur is dependent on the ambient hydrostatic pressure, which influences gas solubility and hence buoyancy of the carcass (Allison *et al.* 1991). The presence of various storm-induced sedimentary structures (Wignall 1989) and profuse benthic faunas (Birkelund *et al.* 1983) suggests that water depth was not excessive enough to generate extreme hydrostatic pressures, indicating that re-flotation of the carcass was feasible. Scotchman (1989) estimated that water depths over north-west Europe during the Kimmeridgian were in the range of 10–100 m. Assuming this to be correct, the maximum hydrostatic pressure possible would be approximately 10 atm., based on a surface pressure of 1 atm., and an increase of 1 atm. for every 10 m below the water surface. These pressure levels would not prevent re-flotation of a moderate-sized marine crocodylian carcass (based on experiments by Allison *et al.* 1991).

There may have been some scavenging of the carcass, either during post-mortem drifting in the water column, or after settling on the substrate. The cause of death cannot be ascertained.

The skull became separated from the rest of the carcass either in the water column or on the substrate, and settled with the dorsal surfaces facing upwards (Text-fig. 9B). The dorsal bone surfaces were partially exposed for a period of time to allow an initial epibiont encrustation event in certain areas. Following continued colonization, with low rates of contemporaneous background sedimentation, a sporadic storm event, for which there is abundant sedimentological evidence (Wignall 1989), probably flipped the skull over onto its dorsal surface (Text-fig. 9C). This presumably caused the conspicuous fragmentation and probably resulted in the loss of the posterior and mandibular elements. Another colonization event then commenced on the exposed ventral



TEXT-FIG. 9. Postulated taphonomic history of the skull of *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, the carcass falls to the substrate; B, skull is detached from the body, soft tissues decay, and dorsal surface is encrusted; C, skull is flipped over on to its dorsal surface, mandible and posterior skull elements are lost, and ventral surface is encrusted; D, skull is further fragmented; E, sediment washes over, overburden pressure deforms the skull, and burial proceeds.

surfaces, in addition to further fragmentation (Text-fig. 9D). The encruster relationships do not indicate whether the substrate was continually oxic during these colonization events, or whether intermittent phases of anoxia occurred.

Abrasion on the ventral surface and on the epibionts suggests that a period of intense sediment-laden storm-current activity prevailed, before the skull was completely covered with sediment and subsequently deformed by overburden pressure (Text-fig. 9E) during burial.

A specimen of *Pliosaurus brachyspondylus* (BRSMG Cc332) collected at approximately the same stratigraphical level at Blue Circle Industries plc, Westbury Works in 1980 (Taylor and Cruickshank 1993), and a new skeleton of this genus discovered during the summer of 1994 from the same locality (Carpenter 1995), provide further evidence for horizontal deformation episodes that follow carcass burial. In these skulls, a similar distortion in the maxillary region can be seen. Deformed skull material is also common in Callovian marine crocodile material (pers. obs., DRG). Post-depositional processes, such as mass movement on an inclined substrate, or possibly the overburden pressure from wet sediment engulfing skull elements, are likely to have been responsible for deforming the bone in a plastic manner. Such processes seem to have occurred commonly in comparable marine mudstone facies (Martill 1986).

#### CONCLUSIONS

Metriorhynchid crocodylian remains are rare in the English Kimmeridgian, and only three reasonably well preserved skulls have been identified. Micro- and macro-epibiont communities on a new skull from the Lower Kimmeridgian of Westbury, Wiltshire testify to a complex taphonomic history, involving two phases of colonization. The absence of similar bone surface communities in other contemporary marine reptiles from the same locality (Taylor and Cruickshank 1993), indicates that encrusting episodes are localized, and influenced by sediment dispersal and rate of burial.



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